Socioecological Effects of Long-Term Grooming Symmetry and Asymmetry in Eastern Female Chimpanzees *(Pan troglodytes schweinfurthii)*

by Lara McCallister

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Thesis directed by

Carson Murray
Associate Professor of Anthropology

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Dedication

This thesis is dedicated to my father, Todd McCallister, who passed away shortly before I started my graduate education at The George Washington University. I became interested in behavioral economics and reciprocity in non-human primates because of his dissertation work on game theory, and his decades-long career in economics. I hope this thesis provides a new spin on an academic passion that he carried throughout his life.

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Chapter 1: Introduction

Cooperation–prosocial behaviors that benefit a conspecific (Sachs et al., 2004; Nowak, 2006)– is widespread in the animal kingdom. Even creatures phylogenetically distant from mammals, such as micro-organisms, show possible evidence of cooperation (Crespi, 2001; as cited in Schweinfurth & Call, 2019). Despite the taxonomic breadth of cooperative behaviors, early evolutionary theorists found altruistic behavior difficult to reconcile within the theory of natural selection (Darwin, 1859; as cited in Dugatkin, 1997). This is, in large part, because of exploitation risks by noncooperators (Sachs et al., 2004; Osiński, 2009). If noncooperators exploit benefits from an interaction without giving something in return, the cooperator's fitness decreases. As such, in an attempt to explain the ultimate functions of cooperative behavior, researchers have introduced several influential theories, including reciprocity and reciprocal altruism.

Reciprocity and Reciprocal Altruism

While the definition of reciprocity is not applied uniformly across research areas, the term generally describes a conditional act with the expectation of a return (Guevara et al., 2023). A common type of reciprocity used to explain the ultimate functions of cooperation is reciprocal altruism.

Reciprocal altruism theory posits that an individual will perform a costly service for a conspecific to receive a future benefit in return (Trivers, 1971; Alexander, 1974). The costs incurred by the giver are mitigated by the benefits received, increasing the fitness for both parties involved in a reciprocal exchange (Trivers, 1971; Alexander, 1974; Molesti & Majolo, 2017). Debated evidence of reciprocal altruism is documented across a wide range of taxa, including fish, polychaetes (Taborsky, 2001; Peña et al.,

2020), rats (Rutte & Taborsky, 2007), wild vampire bats (Wilkinson, 1984), olive baboons (Packer, 1977), and chimpanzees (Newton-Fisher & Lee, 2011). Ontogenetically, reciprocity in humans becomes a normative social rule by the time a child is six years old (Wörle & Paulus, 2019) and reciprocal altruism is widely observed in hunter-gatherer communities via food-sharing behaviors (Gurven, 2004). Yet, some debate exists about the prevalence of reciprocal altruism in the animal kingdom (Silk, 2013). To understand the heart of this debate, one must understand the requirements set forth for cooperative exchanges to be considered as reciprocal altruism.

Investigation into the Requirements for Reciprocal Altruism

To be classified as reciprocal altruism, there are several key requirements. Mainly, the giver and receiver in a reciprocal exchange must: a) recognize one another; and b) interact frequently over time (Trivers, 1971). There must also be a time lag between exchanges; i.e., the time between an individual giving a costly service and receiving a benefit in return must be temporally mediated (Schino & Aureli, 2010). This ambiguous "time lag" is important, as it has never been formally operationalized in the reciprocity literature. That said, several primatological studies have tested if nonhuman primates give and receive only in quick temporal succession or if they reciprocate over more extended periods of time. The former–referred to as short-term reciprocity– has been studied within bouts (Manson et al., 2004) and within days (Koyama et al., 2006). The latter, henceforth referred to as long-term reciprocity, has been studied over much longer time intervals, with some research spanning over a decade (Silk et al., 2006).

Some argue that reciprocity over longer timescales is impossible in some species because of cognitive constraints on social memory (Stevens & Hauser, 2004). In other

words, the time lag between giving and receiving required in some reciprocal exchanges might not be possible for animals with lower social memory capabilities (although, see Schweinfurth & Call, 2019; Brosnan, 2024). That said, cognitive and field studies in nonhuman primates provide evidence for long-term reciprocity in macaques (Schino et al., 2007), baboons (Frank & Silk, 2009), and chimpanzees (Gomes & Boesch, 2009). Another example of a long-term reciprocation study was performed by Schino & Pellegrini (2009) in mandrills. Schino & Pellegrini (2009) found that female mandrills exhibited long-term reciprocal partner choice in grooming exchanges, even when short-term, immediate reciprocation was controlled for in the analysis. Thus, mandrills are basing their decisions to reciprocate on long-term reciprocal interactions.

As highlighted above, nonhuman primates (NHPs), are an ideal order to study long-term reciprocity, as several primate species are more likely to give and receive contingent-based exchanges over longer versus shorter time intervals (Jaeggi et al., 2013). In particular, species characterized by high fission-fusion social organizations, in which subgroups change composition regularly, face different socio-cognitive pressures as relates to reciprocity. In addition, primates exhibit a particular social behavior ideal for long-term reciprocity: social grooming. Social grooming is advantageous for several reasons; it is a form of low-risk reciprocity (Brosnan & de Waal, 2002) that incurs a low cost for the giver, while providing both physiological (Akinyi et al., 2013) and social (Dunbar, 1991) benefits for the receiver. For example, grooming aids in the removal of ectoparasites (Zamma & Nakamura, 2015), releases beta-endorphins that encourage social bond attachment (Keverne et al., 1989), helps with stress management (Cheney & Seyfarth, 2009), and strengthens social bonds (Dunbar, 2010). Since it is low-cost and

high-reward, it is a widespread currency and service in the primate order (Dunbar, 1991; De Waal, 1997) that can be traded for coalitionary support (Newton-Fisher & Kaburu, 2017), meat sharing (De Waal, 1997), or for reciprocal grooming (Henazi & Barrett, 1999). Given its prevalence, low-cost, high benefit, and trading value as a biological commodity (Noë & Hammerstein, 1994), social grooming symmetry between primates is commonly used to investigate changes in giving and receiving over different time intervals.

One particular study of interest researched long-term grooming symmetry by investigating how, if at all, reciprocation changed over time in wild chimpanzees. Chimpanzees are characterized by high fission-fusion dynamics (Aureli et al., 2008), making long and short-term reciprocity of great interest. After analyzing grooming bouts from a population of western chimpanzees (*Pan troglodytes verus*), Gomes et al. (2009) found a positive correlation between grooming given and received over a two-year period. Furthermore, rates of giving and receiving were more symmetrical when examined over longer time intervals as compared to reciprocity observed within bouts or throughout the day. Although Gomes & colleagues (2009) provided a robust interpretation of long-term grooming reciprocation, unanswered questions still remain. For example, although the paper investigated long-term grooming *symmetry* (i.e., long-term reciprocation) using sex, relative rank, and social bond status as predictors, the paper did not test how socio-ecological factors such as these influence grooming *asymmetry* over longer time intervals. Socio-ecological factors were treated as a *control* to test grooming symmetry, not as a tool to investigate factors leading to asymmetry. In addition, kinship was excluded, and the interaction between socio-ecological factors such

as relative and absolute rank were not explored. While this was not part of the scope of the Gomes et al. (2009) paper, these lines of inquiry still hold importance for understanding what socio-ecological factors influence and discourage long-term reciprocity.

Population-level sex differences in sociality among chimpanzees offer an important avenue of investigation. The Gomes et al. (2009) study included both male and female western chimpanzees in their sample. Female eastern chimpanzees, in particular, show behavioral differences from their western counterparts that may have important implications for long-term reciprocation. Although all chimpanzees are characterized by a fission-fusion social organization and female-biased dispersal (Kahlenberg et al., 2008; Fox et al., 2022), eastern females are less gregarious than western females (Wakefield, 2008). These differences in gregariousness are reflected in the use of their respective home ranges. Both male and female western chimpanzees use all areas of their home range equally. Consequently, western chimpanzees frequently interact with other males and females within their home range (Lehmann & Boesch, 2005). In contrast, eastern female chimpanzees establish overlapping core areas within home ranges and spend less time with other females compared to their western counterparts (Lehmann & Boesch, 2005). Still, despite the amount of time eastern chimpanzee females spend alone, they show evidence of weak (Fox et al., 2022) and strong (De Waal, 1984) social bond formation with non-kin (Foerster et al., 2015). Likewise, emerging evidence suggests females might have reason to invest in intrasexual relationships. Females who were more socially integrated in the year before parturition had higher offspring survival (Feldblum et al., 2025). Applying this research to the current line of inquiry, long-term grooming

symmetry might be a means to form or maintain strong social relationships among eastern chimpanzee females who do not interact frequently with other conspecifics. Intersexual grooming relationships might also be beneficial for female eastern chimpanzees. According to the social dominance hypothesis, adolescent chimpanzee males are more aggressive to females than male conspecifics, suggesting that all females are lower-ranked than male members of a community (Enigk et al., 2021). As such, eastern female chimpanzees might give more grooming to higher-ranked males in order to curry favor and lessen aggression risk. This thesis is driven by these ideas on intrasexual and intersexual relationships.

Aims and Predictions

This thesis investigates the socioecological correlates of grooming symmetry among lactating eastern female chimpanzees at Gombe National Park, Tanzania. Based on chimpanzee socioecology, I predict that: (1) Relatively lower-ranking females will give more grooming than they receive from higher-ranking females to "groom up the hierarchy" (Tiddi et al., 2012) and gain preferential access to resource-rich core areas (Pusey & Schroepfer-Walker, 2013; Miller et al., 2014). To avoid risk of aggression from males (Stumpf & Boesch, 2006; Enigk et al., 2021), I predict that: (2) Females will give more grooming than they receive to high-ranking males. In line with Hamilton's (1964) kin selection theory–which posits that individuals will perform altruistic acts for their kin–I predict that: (3a) Females will give more grooming to female kin compared to non-kin, and (3b) Females will give more grooming to male kin compared to non-kin.

Chapter 2: Methods

Study Site

Gombe National Park is a 35 km^2 mountainous habitat in the Kigoma Region of Northwestern Tanzania (Pusey et al., 2007), that is restricted by Lake Tanganyika on the west and a rift system on the east (Pusey et al., 2005). Within this park, chimpanzees at Gombe occupy mosaic environments of riparian forests, woodlands, and grasslands (Pusey et al., 2005, 2008).

Chimpanzee communities within Gombe are divided into north, central, and southern regions (Pusey et al., 2007). Although originally, two communities inhabited the central region–Kasakela and Kahama, respectively–male intrasexual aggression led to the Kahama community's extinction in 1977 (Goodall, 1986; as cited in Pusey et al., 2007). During the course of this study period (1976-2015), there were three established chimpanzee communities at Gombe: Mitumba in the north, Kasakela in the middle, and Kalande in the south (Pusey et al., 2007).

Study subjects for this thesis are a part of the Kasakela community. Dr. Jane Goodall collected observational data on this community beginning in 1960 (Pusey et al., 2008). Almost all individuals within the community were identified by 1964 (Walker et al., 2018), with full identification available two years later (Pusey et al., 2007). Starting in 1974, field research assistants collected minute-by-minute grooming focal follow data on individuals in Kasakela, making it an ideal sample for long-term behavioral analysis (Wilson, 2012).

Study Population

Females with grooming data from at least one six-month interval from 1976-2015 were included in the analysis (**Table 1**, **Table 2**). To ensure robusticity and validity, a female that groomed for less than 20 minutes throughout a given six-month interval was excluded from the study. These criteria resulted in 22 focal females in intrasexual relationships and 24 focal females in intersexual relationships. While grooming symmetry based on dyads is of interest, I summarized data based on conspecific sex and rank classes due to low observation times for many dyads in the six-month bins.

Table 1: Number of six-month intervals per individual in intrasexual relationships.

Focal ID	***N* Six Month Interval**
BAH	3
DL	8
EZA	3
FF	10
FN	12
GA	12
GLD	9
GLI	7
GM	11
IMA	5
NUR	8
PI	8
PL	1
PM	1
PS	1
SA	9
SI	3
SR	1
SW	6
TG	6
TZ	1
WK	1

Table 2: Number of six-month intervals per individual in intersexual relationships.

Focal ID	*N* Six Month Interval
AT	2
BAH	8
CD	1
DL	7
EZA	6
FF	20
FN	19
GA	4
GLD	2
GLI	1
GM	9
IMA	4
KD	1
MF	2
NUR	5
PI	6
PL	2
SA	9
SI	3
SW	9
TG	9
TTA	1
TZ	5
WK	8

Grooming Data

To investigate if dominance rank and relatedness influence grooming symmetry, I used a dataset that focused on mother and infant behavior. Since 1970, the mother-infant dataset has compiled minute-by-minute focal follows of a mother and, if applicable, her two youngest offspring (Murray et al., 2014). Group composition data among focal females is also recorded every five minutes. A myriad of behaviors are recorded during these follows, such as feeding, play, and grooming (Murray et al., 2014).

Using the mother-infant dataset, Lo & Markham (2018, unpublished data) compiled grooming data on lactating females from 1976-2015. Each minute of grooming data indicated the age and sex of a female and her grooming partner. Any grooming

partner less than 11.5 years of age (Walker et al., 2018) was excluded from the sample pool, as any individual younger than this has not reached sexual maturity. This exclusion was to prevent skew in results due to mother-infant interactions.

Six-Month Intervals

Minute-by-minute dyadic grooming data were divided into six-month intervals from 1976-2015, with 40 total six-month intervals included in intrasexual (F/F) analysis, and 52 intervals in intersexual (M/F) analysis. Grooming symmetry intervals started and ended in accordance with wet and dry seasons. During dry seasons, female chimpanzees demonstrate increased active periods (Lodwick et al., 2004), smaller group sizes, and differences in foraging strategies (Murray et al., 2006) compared to the wet seasons. As such, creating six-month intervals based on season was integral to account for possible behavioral differences due to food availability. At Gombe, dry seasons occur from May to October (Clutton-Brock & Gillett, 1979). The first six-month interval included in the analysis started in the wet season in 1976 and ended in April 1977, the second from May 1977 to October 1977, and so on.

Predictor Variables

1. Dominance Rank

To calculate rank over time, Foerster et al. (2016) assessed pant-grunt vocalizations using Maximum Likelihood Fitting (MFT) and created Elo-scores. Elo-scores are a common technique to assess rank using point estimates in agonistic interactions (Newton-Fisher, 2017). Categorical ranks were determined from normalized Elo-scores using the Jenks Natural Break method (Walker et al., 2018). Using the same Elo-scores implemented in Foerster et al. (2016) and lactating female grooming data (Lo

& Markham, 2018), a new database was created that linked Elo-scores for females and their grooming partners to each grooming bout during the data collection period.

2. Relatedness

Relatedness was determined based on long-term demographic records from the study site. Given equivocal evidence for paternal kin recognition and behavioral biases, I categorized relationships based on maternal relatedness.

Calculating Grooming Symmetry Over Time

To operationalize female grooming symmetry, the number of minutes a female gave grooming was weighed with the number of minutes they received it. To achieve this, the total minutes a female engaged with partners (e.g., high-ranking male, relatively lower-ranking female) were added together within a given six-month interval. These totals were then divided into the number of minutes a female gave, received, and mutually groomed conspecifics of these respective categories. These values were inputted into the following equation:

$$Grooming\ Symmetry(x) \quad = \frac{Received - Given}{Given + Received + (2 \times Mutual)}$$

In this equation, x represents a grooming partner of a given socioecological subcategory (e.g, high-ranking males/females, male/ female maternal kin/nonkin).

Grooming symmetry scores were continuous and bounded from -1 to 1. A score of -1 indicated negative grooming asymmetry; the lactating female only served as the groomer for a given six-month interval without receiving any in return with a given partner sex-relatedness class. Conversely, a score of 1 signified positive grooming asymmetry; the female only received grooming from individuals of a given socio-ecological bin for a given partner sex-relatedness class. A score of 0 represented

"grooming symmetry"; that is, there was equal occurrence of giving and receiving between an individual and conspecifics of a socio-ecological category during a given six-month period.

Statistical Analyses

To test the socioecological correlates of grooming symmetry, estimations were calculated for both intrasexual and intersexual subdatasets using a Generalized Linear Mixed Effects Model (GLMM) with the lme4 package in R (Bates et al., 2015). See **Table 3** for model parameters.

Table 3: Models and parameters for linear analysis.

Model	Response Variable	Fixed Effects	Random Effects
Intrasexual Model	Symmetry Score	Dominance Rank Maternal Relatedness Total Grooming Time	Individual ID Six-Month Interval
Intersexual Model	Symmetry Score	Dominance Rank Maternal Relatedness Total Grooming Time	Individual ID Six-Month Interval

In the intrasexual model, fixed effects included relative rank, maternal relatedness, season, and total focal grooming observation time per six-month interval. The intersexual grooming model used the same fixed effects, with the exception of rank; female relative rank was replaced with male absolute rank.

Since the response variable (grooming symmetry score) was a bounded continuous variable ranging from -1 to 1 and included 0, it limited the options for selecting an appropriate error distribution family. Although raw data results revealed a

non-normal distribution, a Gaussian error distribution family was applied to the models (for justification of this approach, see Knief & Forstmeier, 2021).

To test model assumptions, the DHARMa package in R was used to simulate residual data (Hartig et al., 2024). Both the intrasexual and intersexual model did not show violations of assumptions. As such, I report original model results in subsequent sections.

Table 4: Predictions and results table.

Prediction	Do Results Support Predictions?
1. Lower-ranking females will "groom up the hierarchy."	X
2. Females will give more grooming than they receive to high-ranked males.	X
3a. Females will give more grooming to female kin compared to non-kin.	X
3b. Females will give more grooming to male kin compared to non-kin.	✓

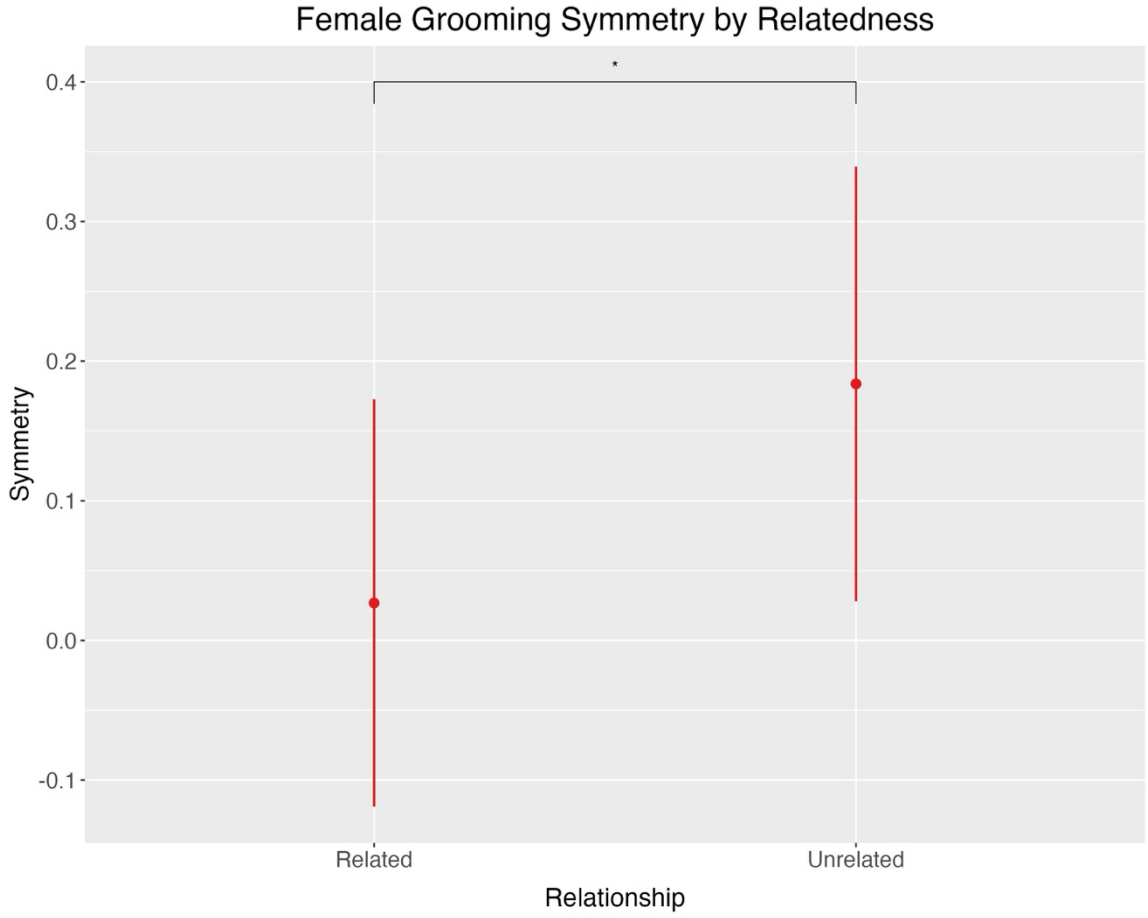
Intrasexual Grooming: Dominance Rank and Relatedness

In the intrasexual grooming model (**Table 5**), I analyzed the effects of dominance rank and relatedness on female-female grooming symmetry. When examining dominance rank, there was no significant difference in symmetry scores. This was not the case with relatedness; females were more likely to receive grooming from unrelated individuals compared to related individuals (β=0.157, SE= 0.073, p=0.034, **Figure 1**).

Table 5: Intrasexual model summary with socioecological predictors of dominance rank, maternal relatedness, and grooming time.

Predictors	Estimate	Standard Error	t value	Pr(>|t|)
(Intercept)	-0.013	0.084	-0.160	0.874
Lower Rank than Grooming Partner	-0.109	0.074	-1.463	0.146
Same Rank as Grooming Partner	0.051	0.084	0.601	0.549
Unrelated	0.157	0.073	2.150	**0.034**
Total Grooming Observation Time	<0.001	<0.001	1.302	0.195

Figure 1: Female Grooming Symmetry with Females by Relatedness.



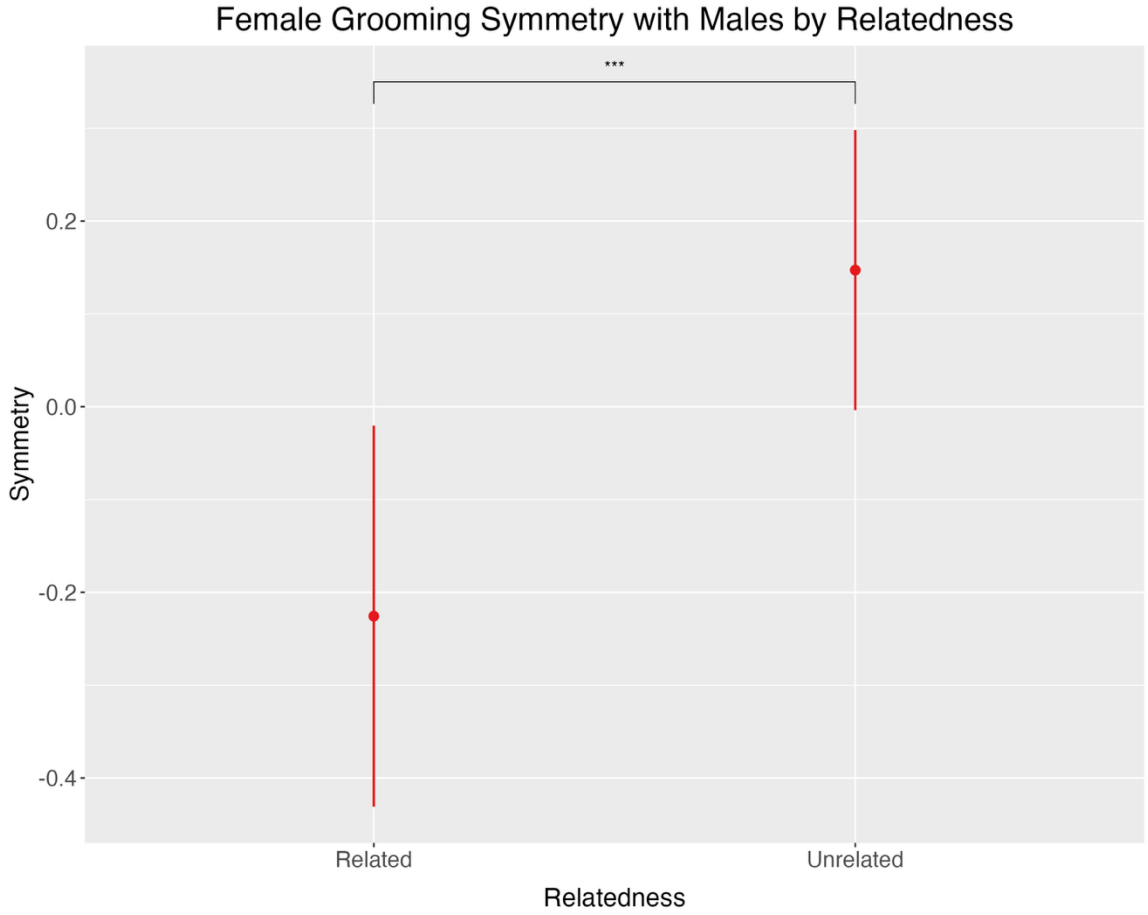
Intersexual Grooming: Dominance Rank and Relatedness

In the intersexual model (**Table 6**), I examined the effects of relatedness and male dominance rank on female grooming symmetry. Although females only gave grooming to males of every rank, the intersexual model did not indicate a significant difference in grooming scores when dominance rank was a sole predictor. Yet, like the intrasexual model, there was a significant difference in relatedness (β=0.373, SE=0.083, $p<0.001$). Females received grooming from unrelated males, and exclusively gave grooming to related males (**Figure 2**).

Table 6: Intersexual model summary with socioecological predictors of dominance rank, maternal relatedness, and grooming time.

Predictors	**Estimate**	**Standard Error**	**t value**	**Pr(>|t|)**
(Intercept)	-0.258	0.126	-2.294	**0.023**
Unrelated	0.373	0.083	4.483	**<0.001**
Low Rank	-0.140	0.085	-1.641	0.103
Mid Rank	-0.082	0.065	-1.262	0.209
Total Grooming Observation Time	<0.001	<0.001	0.767	0.445

Figure 2: Female Grooming Symmetry with Males by Relatedness.



Differentials Across Partner Sex

Because females exclusively gave grooming to males regardless of rank, I conducted an additional analysis to investigate whether there were sex-based differences in grooming symmetry (**Table 7**). When running a model based on grooming partner sex and relationship as sole predictors (but creating reciprocity scores based on combined predictors in both the intersexual and intrasexual model), there was a statistically significant difference between intrasexual and intersexual grooming relationships (**Figure 3**, **Figure 4**). Females were more likely to have grooming symmetry in intrasexual grooming relationships, and to exclusively give grooming in intersexual relationships (β=-0.170, SE=0.049, $p < 0.001$). It is important to note that when relative and absolute

dominance rank are included in the model, this significance no longer applies. That said, females are more likely to receive grooming from unrelated individuals across intrasexual and intersexual grooming relationships (β=0.280, SE=0.055, p <0.001).

Table 7: Partner sex model summary with socioecological predictors of maternal relatedness and grooming time.

Predictors	**Estimate**	**Standard Error**	**t value**	**Pr(>|t|)**
(Intercept)	-0.075	0.064	-1.171	0.246
Partner Sex: Male	-0.170	0.049	-3.491	**<0.001**
Unrelated	0.280	0.055	5.113	**<0.001**
Total Grooming Observation Time	<0.001	<0.001	1.479	0.140

Figure 3: Female Grooming Symmetry by Sex.

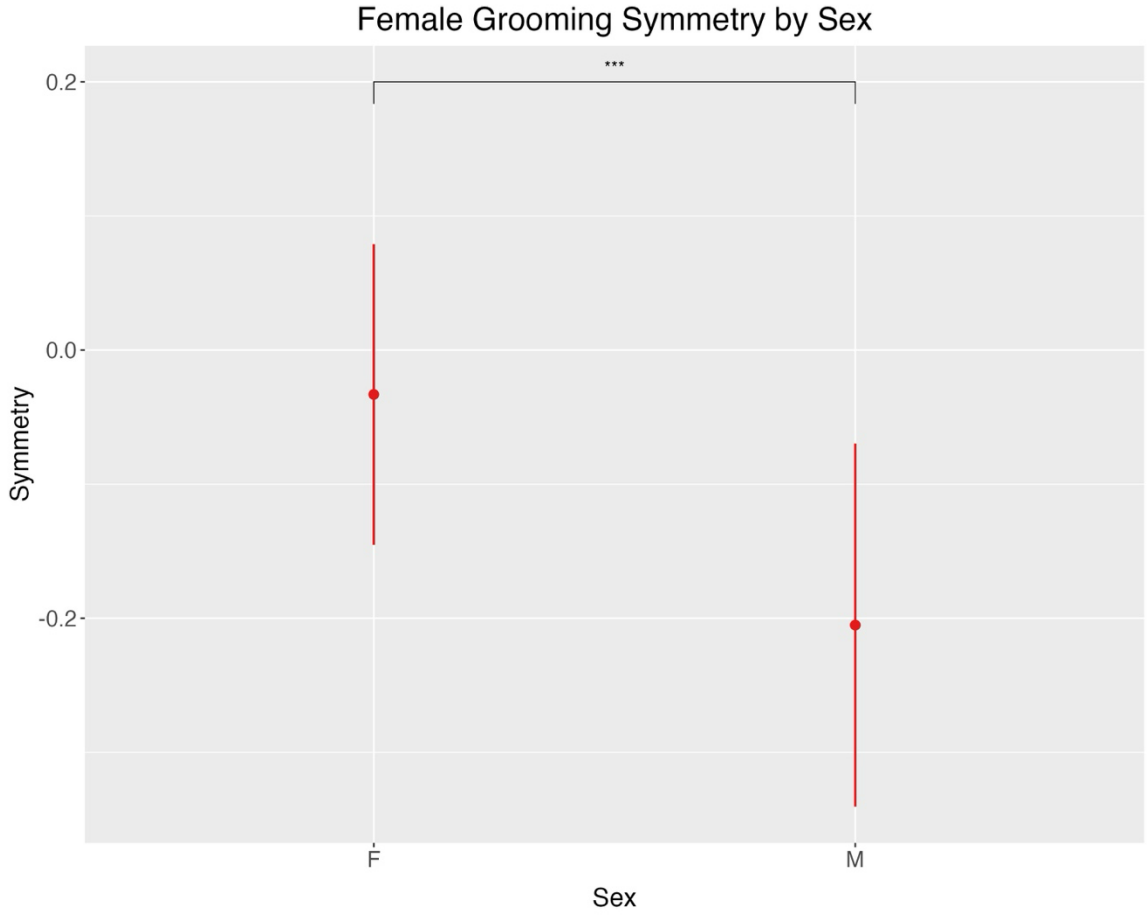
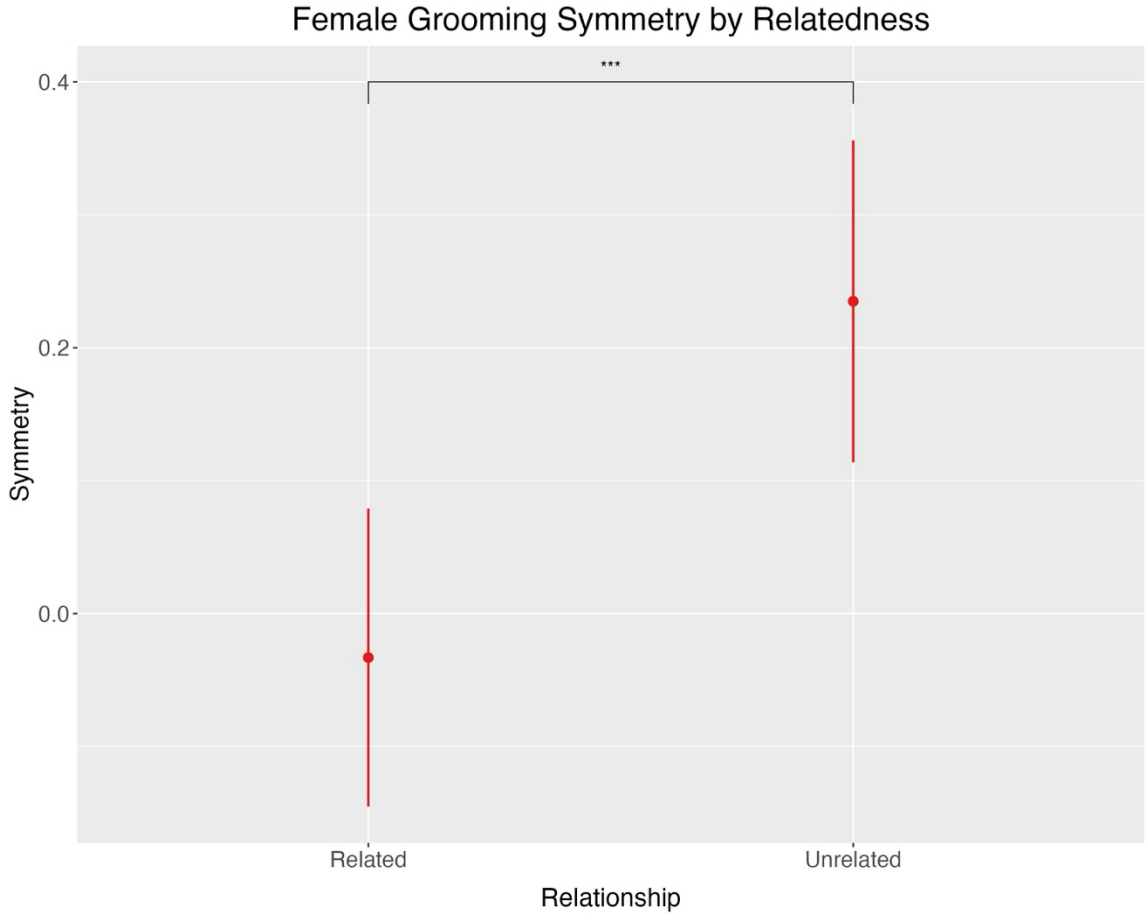


Figure 4: Female Grooming Symmetry by Relatedness Across Sex.



Chapter 4: Discussion

This thesis investigated the effects of socioecological factors—dominance rank and relatedness — on grooming symmetry over six months. Results both confirmed and conflicted with predictions, as outlined below.

Dominance Differentials and Grooming Symmetry

Relative and absolute dominance rank did not significantly affect grooming symmetry scores in the intrasexual and intersexual models. In the intrasexual model, I predicted that lower-ranking females would groom up the hierarchy, based on research suggesting possible association patterns between high and low-ranking female chimpanzees (Foerster et al., 2015). In the intersexual model, I predicted that female chimpanzees would groom up the hierarchy and groom high-ranking males to provide protection against aggressive encounters (Enigk et al., 2021). A possible explanation for these null results could be that several females were only recorded grooming for one six-month interval. More data might increase the robustness of results, warranting future investigation.

Grooming Symmetry by Relatedness

In examining the relationship between relatedness and grooming symmetry, I predicted that females would give more grooming to relatives than they receive. Results from the intrasexual model do not support this prediction. Although the intrasexual grooming score with female relatives is close to 0, i.e., symmetrical grooming, the confidence intervals span both positive and negative values. Past research suggests that female offspring benefit from shared space use and rank inheritance from their mothers (Walker & Pusey, 2020). Future research should expand upon this to see if the same

effects are found with female relatives to affirm or disprove the incongruent results presented here.

That said, intrasexual model results revealed that lactating females almost exclusively receive grooming from unrelated individuals. Given that the average interbirth interval for a newly immigrated female is 3.75 years (Walker et al., 2018), most lactating females in this data sample are likely residents of the Kasakela community. There are important behavioral dynamics between immigrant and resident females to consider for future research that may clarify results presented here. Immigrant females often face aggression from female natal group members (Murray et al., 2007). Likewise, immigrant female chimpanzees are more likely to settle closer to lower-ranking female core areas as opposed to higher-ranking female core areas, thereby reducing resource competition and aggression (Murray et al., 2007). Perhaps relatively higher-ranking females receive more grooming from resident or immigrant female conspecifics to curry favor, have access to resources, and lessen aggression risk.

Lactating females may also receive more grooming from non-relatives because they are attractive social partners. As noted earlier, in other chimpanzee populations, female-female social bonds are very common and mostly formed with non-kin (Langergraber et al., 2009). Although female gregariousness is lower at Gombe, accumulating evidence underscores the importance of female-female social bonds among eastern chimpanzees. As such, female chimpanzees might curry favor to establish a cooperative relationship or gain a social bond partner. Future research should explore social bonds further (Fox et al., 2022), especially since female grooming patterns are an indicator of spatial overlap and affiliative relationships (Foerster et al., 2015).

Considering female-male grooming relationships, I predicted that females would give more grooming to male relatives than they receive. The intersexual model supports this prediction; all females in the data sample only gave grooming to male relatives throughout the entire study period. This is in line with previous research suggesting that mothers have an increased social investment in male offspring (Murray et al., 2014). Beyond a mother-offspring relationship, females might invest in relationships with adult male relatives for future defense in agonistic or aggressive interactions. A recent study supports this claim; mothers are more likely to associate with their brothers and sons shortly after giving birth, perhaps to mitigate the risk of infanticide (Wellens et al., 2022). Future studies should clarify these results by looking at male-biased kin investment over longer time intervals, focusing on both nulliparous and parous females.

Grooming Symmetry by Sex

Given the results of the intrasexual and intersexual grooming models, I ran an additional model to investigate sex-based differences in grooming symmetry. When I ran a model with sex and relationship as predictors (with symmetry scores based on all predictors from the intrasexual and intersexual models), the results showed that females gave more grooming to males compared to female conspecifics. These results could be because females curry favor with males to reduce aggression risk (Enigk et al., 2021). In addition, females received more grooming from unrelated individuals than from related individuals. These results suggest that lactating females are attractive social partners to non-relatives across intersexual and intrasexual relationships.

Socio-Cognitive Implications

These results hold important implications for understanding the socio-cognitive social memory capacities and decision-making of great apes. While the cognitive internal representations and abstractions underlying great ape relationships are heavily contested (Povinelli, 2020), there is promising research on great ape socio-cognition. An example of this is in social memory; researchers discovered chimpanzees and bonobos have the ability to remember conspecifics for up to 25 years (Lewis et al., 2023). With this in mind, understanding chimpanzee relationship dynamics through cooperative exchanges could provide key insight into how chimpanzees assess and manage relationships within a fission-fission social structure. This is especially the case for female chimpanzees at Gombe, who are less gregarious than western female chimpanzees (Wakefield, 2008). Significant differences in interactions between maternal relatedness in both males and females could suggest a cooperative proximate mechanism of emotional book-keeping, whereby individuals cooperate based on their affiliative relationships with conspecifics (Zijlstra et al., 2021) that last despite long time intervals apart. Conversely, these exchanges could be tracked based on social memory of past interactions, implying a type of calculated reciprocity (Brosnan & de Waal, 2002). While the former would suggest that female chimpanzees base their reciprocal interactions on their relationship with conspecifics, the latter would suggest that equality drives grooming relationships. Results of this thesis cannot rule out either possibility, but simply suggest that long-term relationships might yield important insight into the socio-cognitive mechanisms underlying affiliative relationships in female chimpanzees.

Chapter 5: Conclusion

This thesis set out to investigate socio-ecological correlates of grooming symmetry in lactating eastern female chimpanzees. In contrast to the Gomes et al. (2009) study, there are several influential socio-ecological factors in symmetry that warrant future investigation. Results show that lactating females benefit from relationships with unrelated conspecifics, invest in their male offspring, and demonstrate sex-based differences in grooming symmetry. Still, there is more work to be done to solidify these findings; in western chimpanzees, research shows that long-term reciprocation is highest when analyzed over a 22-month period (Gomes et al., 2009). As such, a logical future direction of the current thesis should investigate the socio-ecological correlates of grooming symmetry in female eastern chimpanzees over longer time intervals, to determine if these socio-ecological effects truly led to grooming asymmetry, or if there is not enough time in the study period to assess symmetry.

That said, this study is novel in its investigation and implementation. Specifically, the formula adapted for this thesis allows for stream-lined aggregation of grooming data applicable to a wide array of time intervals (e.g., bout, day, month(s), year(s), but see Silk et al., 2006). Researchers can also apply this formula to grooming frequency within dyadic or triadic pairs (assuming an adequately-sized data pool), making it a useful tool for an area of research important in understanding cooperative behaviors and the social world of a myriad of social animals like chimpanzees.

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